



INTERNATIONAL JOURNAL OF
**COMPARATIVE
PSYCHOLOGY**

Published by
The International Society
for
Comparative Psychology

VOLUME 9, NUMBER 4

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SUBSCRIPTION inquiries and subscription orders to institutions and individuals who are not Society members should be addressed to International Society for Comparative Psychology, P.O. Box 1897, Lawrence, KS 66044-8897, USA, Telephone 913-843-1221, or Fax 913-843-1274. Subscription inquiries and subscription orders for Society members should be addressed to Sally McFadden, Managing Editor IJCP, The Department of Psychology, The University of Newcastle, NSW 2308 AUSTRALIA.

Subscription rates:

Volume 9, 1996 (4 issues) \$95.00 (outside the U.S., \$110.00). Members of the International Society for Comparative Psychology receive their yearly subscription as part of their membership dues. For membership information see back pages.

INDEXED OR ABSTRACTED IN: Psychological Abstracts.

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MUTUAL BEHAVIORAL ADAPTATION OF PARTNERS IN DYADS IN TWO SPECIES OF PROSIMIANS

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ABSTRACT: The dynamics of mutual behavioural adaptation in the process of establishing social relationships in mouse lemurs (*Microcebus murinus*) and pygmy slow lorises (*Nycticebus pygmaeus*) was studied. Observations were made over a 3-hour period beginning when a male and a female were first placed together during the non breeding season. As well, the behaviour of stable pairs that had been together for more than one year was observed. Behaviour was recorded using the one/zero method with 5-sec intervals. Two stages of the development of social relationships, each with different functional values, were identified. The first stage involved mutual social investigation, the second the stabilization of the social relationship. Differences in the dynamics of social contacts between species members were due to their different social structures. The process of social adaptation of behaviour in dyads is discussed and quantitative and qualitative characteristics of breeding pairs and non breeding pairs are compared. It is suggested that a convenient strategy for improving breeding is to replace one of the partners with an experienced animal.

INTRODUCTION

Zoos often face the problem of regulating the social behaviour of animals, especially in cases of a) pair formation for breeding, b) group formation, and c) the introduction of a new individual into a group. Attempts to pair monkeys are often problematic because the incompatibility of the prospective partners may result in a high level of aggression (Bernstein, 1969). The risk of trauma during pairing is considered to be lower in young animals than in adults (Bernstein & Draper 1964; Valery & Symms, 1966), so acquainting animals with each other at an early age is recommended (Bernstein 1969; Bernstein

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& Gordon, 1980; Erwin 1979).

The main difficulty in breeding primates in captivity is to find compatible mating partners. Because the social and sexual behaviour of primates is complicated, normal breeding often is possible only after establishing a harmonious relationship between the prospective partners. Pair formation can be further complicated by the idiosyncratic behaviour of individual animals and by pathological social and reproductive behaviour resulting from captivity. In these cases, changing partners is the main alternative. However, when maintaining genetic diversity is of primary concern, as in breeding threatened or endangered species, this is not always possible. The investigation of the pair formation process must be based on the idea of mutual behavioural adjustment of two individuals. Generally speaking we are interested in getting at the behavioural mechanisms of this process; the work reported here is our preliminary investigation of this problem.

When speaking about the social adjustment of the behaviour of two individuals, we mean that their coexistence is the result of changes in the social reactions of each individual. One may say that two individuals put in one area try to attain some sort of behavioural complementation in order to minimize their social discomfort. The physiological and psychological characteristics of this social discomfort depend on the characteristics of the social behaviour of the species, and may be illustrated by the social structure of the species in nature. During the process of mutual social behavioural adjustment every individual tries to control its partner's social behaviour by some changes in its own behaviour. The aim is to neutralize the partner's undesirable acts and to obtain more desirable ones. In this process an individual uses a behavioural strategy appropriate to its age, sex and the behavioural repertoire of its species.

In this study, behavioural adaptation during the development of social relationships was examined in the mouse lemur (*Microcebus murinus*) and the pygmy slow loris (*Nycticebus pygmaeus*). These species were selected because they display very different social structures in a natural environment (Petter, 1962; Martin, 1972). Female mouse lemurs form a central population and the males, who remain at the periphery, come to the center only during the breeding season. Pygmy slow lorises presumably have individual territories and males enter the females' territories during breeding season; however, the pair may stay together for several weeks, or even months. Thus, one may assume that pygmy slow lorises are able to form more prolonged social relationships than mouse lemurs. It is likely that mutual behavioural

interactions are taking place resulting in the partners adapting to one another.

The present investigation was designed to: (1) compare the processes of behavioural adaptation in these two species with different social structures; (2) determine the behavioural strategies of males and females during the social interaction; and (3) discover which behavioural deviations might prevent animals from forming a breeding pair.

METHOD

Subjects

A total of 24 mouse lemurs (*Microcebus murinus*) and 14 lesser slow lorises (*Nycticebus pygmaeus*) from the Moscow Zoo were studied. In the Moscow Zoo, these two species have been maintained in various types of social relationships: (1) a male and female together over several years; (2) a male and female together during 2-3 breeding seasons; and (3) a male and female pairing for one breeding season only. The best breeding routine for mouse lemurs is the last, while the most successful routine for pygmy slow lorises is the second one.

Pairs in the present study were housed in cages (1.5 x 1.5 x 2.0 m) equipped with two or three wooden nest-boxes and the necessary amount of branches and tree roots. The light/dark cycle was that of the Moscow latitude. In this facility, mouse lemurs fall into torpor in November and arouse in February. A similar cycle has been observed in other facilities in Europe (Martin, 1972).

Procedure

We observed pairs of animals on their very first encounters, new partners that had never seen each other before being placed together. We observed new pairings involving 12 male and 12 female mouse lemurs and 7 male and 7 female lesser slow lorises. Initial observations of new pairs lasted for 3 hours. After a year, during which there had been a breeding season, the formed pairs were observed again when we knew about the breeding success of each pair. These observations lasted for 1 hour. Following these observations we reformed pairs in such a way that non breeding partners were paired with breeding partners. The initial interaction of these new pairs was then observed, and in a year

we were able to determine their breeding success. The entire procedure for each species was as follows:

Mouse lemurs: 1988 - 12 pairs were formed and observed for 3 hours during their initial encounter. 1989 - The breeding success of all pairs formed the previous year was determined and the pairs were observed for one hour. Eight pairs had bred, four had not. We reformed the non breeding pairs with four of the breeding pairs, forming eight new pairs, with one member of each having previously bred. The initial encounters of the animals in these groups were then observed for 3 hours. 1990 year - We observed the eight pairs formed the previous year and determined their breeding success -- all pairs had offspring.

Lesser slow lorises: 1988 - Seven pairs were formed and observed for 3 hours during their initial encounter. 1989 - All pairs formed the previous year were observed for one hour and their breeding success determined; three pairs had not bred. Non breeding pairs were reformed with three breeding pairs, forming six new pairs that were observed on their initial encounters. 1990 - We observed the six pairs formed the previous year and determined their breeding success - only one pair did not breed.

Behaviour was recorded using the one/zero method with 5-sec intervals. All observations were carried out at night under red or green light. Experimental pairings occurred in cages similar to the home cages. To do this, during the day the wooden nest-boxes in which the animals were sleeping were moved from the home to the experimental cage. These wooden boxes (one with a male, the other with a female) were opened simultaneously in the evening, when the animals began to be active. All observations were made during the non breeding season.

Three categories of social behaviour were recorded: 1) social investigation - approaching the partner, sniffing and watching; 2) affiliative behaviour - grooming, long tactile contact, playing, etc.; and 3) aggressive behaviour - from ritualized aggressive displays to direct aggressive acts. Stages of pair formation were determined separately for each pair formed during 1988 and 1989 on the basis of analyses of curves of the dynamics of the partners' social activity. First, differences in reliability were determined for every pair and every form of activity, and then for the average data for breeding and non breeding pairs of both species, using a χ^2 test.

RESULTS

Mouse lemur data

On the basis of qualitative and quantitative (χ^2) analysis of the behaviour of the animals on their initial encounters, we divided the three-hour observation period into three stages. The average duration of each stage was as follows: stage 1 - 15 min; stage 2 - 35 min; stage 3 - 130 min.

The percentage of time spent in different behaviours during each stage of the 3-hour observation period for initial encounters in pairs of mouse lemurs is shown in Table 1. Several differences between animals in pairs that went on to breed and those that did not were observed. The data for males that went on to breed are shown in the top panel of the table. There was no aggressive behaviour at all, and

Table 1. Percentage distribution of different types of behaviour during stages of the 3 hour observation period of initial encounters between members of pairs of mouse lemurs.

	Affiliative	Aggressive	Soc. Invest	Marking	Activity	Inactivity
<i>Pairs that became Successful Breeders</i>						
Males						
Stage 1	0.97	0	6.25	0	75.56	17.22
Stage 2	1.48	0	1.94	0	47.22	49.35
Stage 3	0.17	0	1.39	0.61	39.17	58.67
Females						
Stage 1	0.28	3.33	2.64	0	5.97	87.78
Stage 2	0	4.85	0	0	3.89	90.26
Stage 3	0	4.44	0.22	0	2.72	92.81
<i>Pairs that did not Breed</i>						
Males						
Stage 1	0	0.14	5.56	0	56.25	38.05
Stage 2	5.74	0	1.76	0	57.04	35.46
Stage 3	0.61	0.17	0.33	0	34.72	64.17
Females						
Stage 1	3.06	1.11	3.19	0	20.42	72.22
Stage 2	9.07	11.11	1.02	0	4.63	74.17
Stage 3	0.50	1.22	0.11	0	4.72	93.44

affiliative behaviour increased to its highest level at stage 2, before it declined again. The level of social investigative activity was high at stage 1 and declined thereafter. Marking behaviour was observed only by breeding males, and it occurred only at stage 3. The data for the males that did not breed are shown in the lower part of Table 1. Some aggressive behaviour was observed at stage 1, and after declining to zero in stage 2, it increased to its highest level at stage 3. Affiliative behaviour was at its highest in stage 2, after which it declined. The level of social investigative activity decreased systematically from stage 1 to stage 3. The data for activity (walking and jumping) and inactivity (remaining stationary) were similar in breeding and non breeding males.

For the females that went on to breed (top of Table 1), affiliative behaviour occurred only during stage 1, while aggressive behaviour was present at all stages, being highest at stage 3. The level of social investigative activity was highest at stage 1, absent at stage 2, and observed once more at stage 3. The females that did not breed (bottom Table 1) showed affiliative behaviour at all stages, but the level was highest at stage 2. These females demonstrated aggressive behaviour which was also at its highest level at stage 2. The level of social investigative activity of these females decreased substantially from stage 1 to stage 3.

Table 2. Percentage distribution of the kinds of behaviour that occur in response to the social investigative behaviour of the partner in mouse lemurs.

	Quiet	Soc. Invest.	Affiliative	Aggressive	Move Away
<i>Pairs that became Successful Breeders</i>					
Males	0	12.50	12.50	12.50	62.50
Females	4.17	7.29	5.21	80.21	5.21
<i>Pairs that did not Breed</i>					
Males	9.09	18.18	54.54	0	18.18
Females	27.03	5.41	2.70	62.16	0

Table 2 shows the types of reactions that occurred in response to the social investigative activity of the partner. We see that in the pairs that later became successful breeders, the females responded more aggressively than those in non breeding pairs. In the breeding pairs the level of quiet reactions by the females was lower than in non breeding pairs; non breeding females never moved away from the males. Males

reacted aggressively to females only in pairs that later bred, and the level of affiliative behaviour was lower in breeding than in non breeding males. Males reacted quietly to the social activity of females only in non breeding pairs, while the males that later bred usually moved away from the females.

Data from stable partners, the pairs of mouse lemurs that had been kept together for over a year, are shown in Table 3. In the males, affiliative behaviour was present only in pairs that did not breed; aggressive behaviour and marking behaviour only in the breeding pairs. The only social behaviour displayed by the breeding females was marking, while the females in non breeding pairs showed a high level of affiliative behaviour. Females did not show any aggressive behaviour out of breeding season.

Table 3. Percentage distribution of different forms of activity during the 1-hour observations of stable pairs of mouse lemurs.

	Affiliative	Aggressive	Soc. Invest	Marking	Activity	Inactivity
<i>Pairs that became Successful Breeders</i>						
Males	0	0	1.39	21.11	21.94	55.56
Females	0	2.22	0	16.39	4.4	76.94
<i>Pairs that did not Breed</i>						
Males	33.89	0	1.67	0	37.56	26.94
Females	34.17	0	0.28	0	5.55	60

Pygmy slow loris data

On the basis of qualitative and quantitative analysis of partners' behaviour for the pygmy slow lorises, the three-hour observation period was divided into two stages. The average duration of each stage was: stage1 - 45 min, stage 2 - 135 min. The percentage of time spent in different behaviours during each stage of the 3-hour observation period for initial encounters in pairs of slow lorises is shown in Table 4. For the animals that would later breed (top panels of figure), the affiliative behaviour of both males and females increased from stage 1 to stage 2. Males were aggressive only at stage 1, while aggression in females increased from stage 1 to stage 2. Social investigative activity decreased in both males and females from stage 1 to stage 2. The females showed marking behaviour only at stage 2, but the males' marking behaviour was highest at stage 1 and decreased during stage 2.

Table 4. Percentage distribution of different types of behaviour during stages of the 3-hour observation period of initial encounters between members of pairs of pygmy slow lorises.

	Affiliative	Aggressive	Soc. Invest	Marking	Activity	Inactivity
<i>Pairs that became Successful Breeders</i>						
Males						
Stage 1	2.87	0.69	3.94	1.34	41.39	49.77
Stage 2	23.1	0	1.85	0.69	48.47	25.88
Females						
Stage 1	6.25	0.23	3.29	0	36.44	53.8
Stage 2	20.42	0.56	1.34	0.23	20.83	56.62
<i>Pairs that did not Breed</i>						
Males						
Stage 1	0	2.62	5.77	0.99	48.21	42.41
Stage 2	0.06	1.08	3.15	0.7	34.04	60.96
Females						
Stage 1	0	2.9	0.09	0	10.86	86.14
Stage 2	0	2.93	0.62	0	6.08	90.37

Males were equally active throughout the observation period, while the activity of females decreased during stage 2. Inactivity in females remained stable over time, while in males it decreased during stage 2.

For the partners of pairs that later did not breed (lower panels of table 4), we see that females in such pairs did not show any affiliative behaviour, and males showed affiliative behaviour only at stage 2. In general, the level of aggressive behaviour in the males was initially high and then declined, while for females it did not change greatly across stages. Females did not show marking behaviour, whereas males marked during both stages. Social investigative activity declined across stages, in males but increased for the females.

Table 5 compares the reaction to social investigative activity of partners in pair that would later breed with those that did not. Overall these responses did not differ for males, although only breeding males showed reciprocal social investigative and affiliative reactions. The behaviour of breeding and non breeding females differed to a greater extent. For pairs that did not breed, the females never moved away from the male, but in breeding pairs this reaction occurred frequently.

Table 5. Percentage distribution of the kinds of behavior that occur in response to the social investigative behavior of the partner in pygmy slow lorises.

	Quiet	Soc. Invest.	Affiliative	Aggressive	Move Away
<i>Pairs that Bred Successfully</i>					
Males	20.0	12.22	1.11	6.66	60.0
Females	27.82	2.60	15.65	13.04	40.86
<i>Pairs that did not Breed</i>					
Males	26.08	0	0	8.69	65.21
Females	34.37	2.43	0.69	62.50	0

Table 6. Percentage distribution of different forms of activity during the 1-hour observations of stable pairs of pygmy slow lorises.

	Affiliative	Aggressive	Soc. Invest	Marking	Activity	Inactivity
<i>Pairs that Bred Successfully</i>						
Males	40.95	0	1.24	0.19	47.40	10.22
Females	39.71	0.59	0.19	0	4.75	54.75
<i>Pairs that did not Breed</i>						
Males	16.00	0	1.69	0	5.86	75.65
Females	16.34	0	0.98	0	9.64	73.05

The level of affiliation was higher in breeding than in non breeding pairs, and aggression was more frequent in the females of non breeding pairs.

Table 6 presents the data from the one-hour observation periods of pairs of slow lorises that had been together for more than a year. Males of both breeding and non breeding pairs did not demonstrate aggressive or marking behaviour. Affiliative behaviour was more frequent in breeding than in non breeding males. In females, aggressive behaviour was observed only in breeding pairs and then very infrequently. Affiliative behaviour was higher in breeding than in non breeding females. Activity levels were similar in both groups, but levels of inactivity were higher in the non breeding than in breeding females.

DISCUSSION

Adaptation of social behaviour in species with different social structures

The way in which behaviour changed during the initial 3-hour observation period was divided into three stages for mouse lemurs (Table 1) and two stages for pygmy slow lorises (Table 4). This division was reliable according to a χ^2 criterion. The functional meaning of the first two stages is similar for both species. At stage 1 there is a high level of social investigative activity. Stage 2 can be considered the stage of mutual behavioural adaptation. During this stage the level of aggression in pairs of mouse lemurs and the level of affiliative behaviour in pairs of pygmy slow lorises increases. In the slow lorises the social behaviour of partners does not change much once stage 2 has begun and the pair can be considered to be formed. However, for the mouse lemur, stage 3 is the most important for eventual breeding success. Here the activity of the males and females is separated spatially in the cage and also according to the time of day. There are very few social contacts (except the high level of female aggression) and usually one can see only one animal active in the cage (male or female) while the other one is either in the nest-box or sitting motionless in a corner. The main differences in the behaviour of mouse lemur partners that eventually form breeding and non breeding pairs are: a) affiliative behaviour is seen at all stages for females that do not go on to breed, but is observed only at stage 1 for breeding females; and b) males that later breed do not display any aggressive behaviour at all during the first three hours with their female partners.

From analysis of the reaction to social investigative activity by the partner in these two species, the mouse lemurs appear to have lower thresholds for reacting to the social influence of their partners; they react immediately to social investigative activity. For the pygmy slow lorises, responses to the partner's investigative activity are calmer (less intense). With respect to the behaviour of pairs that would later go on to successfully breed, a high level of affiliative behaviour was observed in the slow lorises, while for the mouse lemurs social interactions were almost nonexistent, consisting only of single instances of interactions between the males in females.

The data from the 10 one-hour observations of the stable pairs (animals that had remained together for one year) of both non breeding and breeding mouse lemurs (Table 3) indicate: a) both males and females of the breeding pairs showed marking behaviour, while non

breeding animals did not; and b) non breeding males and females engaged in affiliative behaviour, whereas members of breeding pairs did not. For the pygmy slow lorises (Table 6), partners in both groups showed affiliative behaviour, although it was higher in the breeding pairs. We suggest that male and female mouse lemurs act independently of one another, with the female taking the main role in this process. We think that there are two social subsystems in this species - one for the male and one for the female, and if they do not combine the animals breed successfully (Vakhrusheva & Meshnik, 1989). This assumption agrees with data from field investigations of mouse lemurs (Martin, 1972; Petter, 1962). On the contrary, for breeding success in pygmy slow lorises prolonged affiliative interactions are necessary, as confirmed by others (e.g. Zimmerman, 1989). However, in some cases, keeping a pair of pygmy slow lorises together for a long time may prevent them from breeding because their social interactions become stereotyped, showing a high level of affiliative behaviour (Welker & Welker, 1989).

We suggest that the mutual behavioural adaptation of two individuals is reached by maintaining behavioural asymmetry between partners, with each individual playing its social role. The social role depends on the sex, age, and social status of the individual. The process of social adjustment differs in pairs of prosimians with different social structures. So in slow lorises, the males and females form pairs by engaging in high levels of affiliative behaviour in order to establish their social relationship. There is no such affiliation in mouse lemurs for whom the process of mutual social adaptation involves the partners remaining separated in space and time of day.

When comparing marking behaviour in breeding and non breeding pairs of lorises and mouse lemurs, we suggest that marking for both species involves an androgenic marking mechanism. In mouse lemurs, where the females are normally aggressive toward the males, marking was high in both partners of stable breeding pairs (Table 3), while in pairs of slow lorises only breeding males engaged in marking (Table 6). For non breeding stable pairs of both species marking was never observed. Although the probability of an androgenic mechanism being involved is consistent with the data from the initial encounters (pair formation) in slow lorises, marking was not observed in either male or female mouse lemurs at that time. It is unclear why the males did not mark at this time, perhaps being placed with another animal was too stressful, or perhaps the females' activity inhibits the male.

Behavioural strategies of males and females

Males. The main difference between the social investigatory behaviour of males and females in mouse lemurs and lorises was the high level of the males' social activity. The social behaviour of males of both species was very similar during stage 1. Later, the level of affiliative behaviour of the lorises became higher.

Females. The level of social activity in females was lower than that of males, and it was the females that determined the process of pair formation in both mouse lemurs and pygmy slow lorises. Mouse lemur females were aggressive toward the males, and breeding was successful when the male was tolerant. In the lorises, the affiliative reactions of the female stimulated further affiliative interactions with the partner.

Deviations in social behaviour which prevent a pair from breeding

We suggest the following causes of initial behavioural incompatibility in pairs of pygmy slow lorises resulting in their inability to breed: (a) the social passivity of the females that did not breed compared with those that did, and (b) a somewhat higher level of aggression by the males that did not breed toward their partners. Both of these were evident at stage 1, soon after the animals were first put together. At stage 2 the non breeding pairs showed a very low level of social investigatory behaviour. Perhaps if the female is socially passive, she does not stimulate the male's social activity. In mouse lemurs, on the other hand, it seems that the high level of aggressive behaviour in females and the high level of social activity in males at stage 1, stimulated the partners to become breeding pairs. At stage 2, females in these pairs were socially active and aggressive, but at stage 3 they became as passive as the males.

The social behaviour of partners of both species that were kept together for more than a year and did not breed was similar. Loris pairs showed low levels of affiliative behaviour, relatively high levels of aggression, and low levels of social investigative activity. Mouse lemurs pairs showed high levels of affiliative behaviour and general social activity. Strictly speaking mouse lemurs do not form pairs because the partner's activity is differentiated in space and time, and it is this behavioural "incompatibility" that guarantees their breeding success.

Methods of social behavioural correction

The main cause of incompatibility between males and females is the inadequate social behaviour of one or both partners during the process of pair formation. The methods for correcting this must be worked out on the basis of the following causes: (1) social passiveness of lesser slow loris females; (2) low levels of aggressiveness of mouse lemur females; (3) low levels of general social activity and relatively high level of aggression in slow loris males; and (4) low levels of general social activity and relatively high level of affiliative behaviour in mouse lemurs males. In general, the main cause of behavioural incompatibility of partners is the absence of appropriate species-specific social behaviour by one partner. As a method of behavioural correction, we replaced the partners of non breeding animals with ones that were well-experienced in social and sexual behaviour. This method is based on the idea that partners mutually control each other's social behaviour. The presence of an experienced partner "refreshes" correct reactions with the help of affiliative and equivalent acts and it acts negatively on "incorrect" behaviour displayed by the non breeding animal.

From the results described above, the following four conclusions emerge.

1. Pair formation is based on the mutual social adaptation of partners. The main purpose of social adaptation is to mould complementary, co-adaptive behaviour.

2. The process of social adaptation during pair formation can be divided into two stages, each one with its own functional significance: stage 1 - social investigation, stage 2 - behavioural adaptation.

3. In pygmy slow lorises and mouse lemurs the first stage is less important than the second, when differences based on the social structure of the species appear.

4. In mouse lemurs the probability of reproductive success is based on the low level of social activity of partners and on the absence of a social structure that we typically think of as a pair. In pygmy slow lorises reproductive success is based on a high level of affiliative behaviour between the partners which provides a real pair formation.

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HAND PREFERENCES IN NEW WORLD PRIMATES

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ABSTRACT: Studies of hand preferences in the platyrrhine species are reviewed. Hand preferences of the New World species have been recorded during feeding activities, visuospatial reaching, haptic discrimination, tool use and in a variety of routine tasks using the hands. Of the New World species tested so far, the common marmoset (*Callithrix jacchus*) and squirrel monkeys (*Saimiri sciureus*), appear to be the only species that do not display handedness in feeding activities: at the population level both species display a symmetrical distribution of hand preferences. It appears that only one New World primate species, the spider monkey (*Ateles geoffroyi*), displays left handedness during feeding while the other species are right handed or have no handedness. Thus, the findings for hand use in feeding do not support the Postural Origins hypothesis of MacNeilage et al. (1987) as it predicts left handedness rather than right in the arboreal platyrrhine species. Overall, the reports of handedness for tasks requiring complex visuospatial or tactile processing in the New World primates concur with those reported for humans, who have left handedness in haptic discrimination and complex visuospatial tasks and right handedness for manipulative tasks. Squirrel monkeys are left handed when reaching for moving objects and capuchins display left handedness in haptic discrimination tasks, and right handedness during sponging tasks. There is strong evidence of an effect of posture on the strength of hand preferences, and some affects of age and gender on hand use have also been reported. However, these variables do not influence hand preferences consistently across species or across tasks conducted with the same species.

INTRODUCTION

This paper reviews the research of hand preferences in the platyrrhine species and evaluates the data from an evolutionary perspective. Handedness is usually defined as the preferential use of one hand over the other in most tasks and in most subjects in a group (McGrew and Marchant, 1993). However, in this review handedness is defined as preferential use of one hand at the population level for tasks

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sharing the same type of perceptual, cognitive and/or motor demands. Handedness was once believed to be a characteristic unique to humans (Warren, 1977; Warren, 1980). However, MacNeilage et al. (1987) challenged this hypothesis, reanalysing a number of studies and revealing asymmetrical distributions, at the population level, of right and left-hand preferences in various nonhuman primate species. MacNeilage et al. (1987) presented the Postural Origins hypothesis as an initial attempt at a unified evolutionary theory outlining how manual specialization (handedness) may have evolved in primates. They proposed that handedness evolved first in the prosimians, the earliest primates, to overcome problems of postural control when feeding. Two specializations were said to have evolved in prosimians; a right hemisphere specialization for the control of simple, visually guided reaching and a left hemisphere specialization for postural control, these specializations being retained by the later evolving primates, both New and Old World species. MacNeilage et al. (1987) hypothesised further that the role of the right hand in postural control may have led to left hemisphere specialization for precise sequential limb positioning and thus fine somatic sensorimotor control. This may have predisposed later evolving primates, less dependent on vertical support, to prefer the right hand for manipulative tasks or tasks requiring fine sensorimotor control. In summary, MacNeilage et al. (1987) postulated the presence of a left-hand preference for visually guided reaching tasks and a complementary right-hand preference for manipulative tasks in both New and Old World primate species, and suggested that the transition from left-hand preferences for simple, visually guided reaching to right handedness for fine manipulation may have occurred in the great apes along with increased bipedal locomotion. Finally, with the advent of predominant bipedalism generalized right handedness may have evolved in humans, according to their hypothesis. Despite the fact that the Postural Origins hypothesis may be contested on the grounds that lateralization of sensory processes had already evolved well before primates (Bradshaw and Rogers, 1993) we will focus our discussion of the hypothesis on motor lateralization in primates.

Prosimians have been found to be left handed when picking up and holding food, supporting the Postural Origins hypothesis (Sanford et al. 1984; Forsythe and Ward, 1988; Masataka, 1989; Ward et al. 1990; Milliken et al. 1991). However, the results of studies examining hand use in feeding activities in Old and New World primates are contradictory. Although some studies report left handedness in feeding (picking up and holding food) for some species (Itani et al. 1963; Tokuda, 1969), there is right handedness in others (Yuanye et al. 1986;

Diamond and McGrew, 1994; Westergaard et al. 1997), and either a symmetrical distribution of hand preferences within groups or no hand preferences in other studies (Warren, 1953; Fagot et al. 1991; Rothe, 1973; Hook-Costigan and Rogers, 1998). When handedness for feeding or grasping has been found for the great apes, mostly chimpanzees, a bias toward right lateral preferences is revealed (Bard et al. 1990; Fagot et al. 1992; Hopkins, 1993; Hopkins et al. 1993; Colell et al. 1995; Hopkins and de Waal, 1995), possibly supporting the hypothesis of MacNeilage et al. (1987). However, other studies of hand use in orangutans and gorillas have found no handedness in feeding despite the existence of preferences at the individual level (Annett and Annett, 1991; Byrne and Byrne, 1991; Rogers and Kaplan, 1996). Therefore, although there is evidence to suggest that prosimians are left handed, consistent with the hypothesis of MacNeilage et al. (1987), the data for hand preferences in apes are either inconsistent or possibly have a tendency for right handedness, at least in chimpanzees. In general, the hand preferences displayed by the New and Old World primates appear to vary between species and studies.

At the time the Postural Origins hypothesis was formulated there were very few studies of hand preferences in the New World species and MacNeilage et al. (1987) based their hypothesis on only 5 studies of the New World primates. Three of these studies examined hand use of the common marmoset, *Callithrix jacchus* (Stellar, 1960; Rothe, 1973; Box, 1977), and the results of these studies were contradictory. Box (1977) reported a tendency toward left-hand preferences for taking and holding food, in a group of 8 marmosets, whereas Rothe (1973) found no bias toward left or right handedness in 21 marmosets tested for hand use in a number of routine activities. In fact, Rothe (1973) reported that most subjects were ambipreferent for the hand use activities. Stellar (1960) recorded the hand used by marmosets to displace an object that covered a food well and found that 4 subjects preferred the right hand, 2 the left and 2 were ambidextrous. The fourth study cited by MacNeilage et al. (1987) examined the hand preferences of 3 cebus monkeys during manipulative activity (Kounin, 1938). Two of the monkeys demonstrated a right-hand preference for manipulatory tasks and one preferred the left hand. The final paper cited examined the hand preferences of 14 squirrel monkeys, *Saimiri sciureus* (Fragaszy, 1983), 6 of these squirrel monkeys displayed significant hand preferences but it was not stated how these hand preferences were distributed. MacNeilage et al. (1987) combined the evidence for the New World primates with that of the Old World primates generating the theory for the combined platyrrhine and catarrhine species, as discussed

previously. However, as these species have evolved as geographically distinct populations and thus different variables may have influenced their evolution, we suggest that New World species should be considered separately.

Since the publication of MacNeilage et al. (1987), there has been a number of studies examining hand use in the platyrrhine species and we will now review them. The data is presented in Tables 1-7 according to the type of task employed. The species, ages of the subjects and individual hand preferences are indicated where possible, but not all of the papers reported all of these variables.

HAND USE WHEN REACHING FOR AND HOLDING FOOD

Lateralized hand use for reaching for and holding food has been recorded in a variety of platyrrhine species (Table 1). Hand use in feeding has been referred to as a "spontaneous" behavioural act as it occurs without experimental manipulation (eg. Rothe, 1973; Diamond and McGrew, 1994). Hand preferences in feeding activities appear to be species-specific.

Marmosets (Callithrix jacchus, Callithrix penicillata)

Studies in the common marmoset (*Callithrix jacchus*) of hand use when taking and holding food, reveal a symmetrical distribution of preferences at a group level. As previously mentioned, Box (1977) reported that 6 of the 8 marmosets she tested were left handed when picking up food, and 5 displayed left-hand preferences when holding food. Matoba et al. (1991) has reported significant left handedness for 46 adult marmosets scored when picking up food (Table 1). A reanalysis of their data comparing their population distribution to chance using the chi square goodness-of-fit statistic, however, failed to find significance ($\chi^2 (2) = 2.65, p > 0.20$, Siegel and Castellan, 1994). In addition, analysis of the distribution of left and right-hand preferences in the male/female subgroups using the chi square goodness-of-fit statistic revealed no significant affects of gender on handedness in the marmoset (males, $n = 23, \chi^2 (2) = 1.13, p > 0.5$; females, $n = 23, \chi^2 (2) = 1.65, p > 0.3$). [The term gender is used throughout this review, rather than the term sex, to indicate that hand preferences may be influenced by differences in the behaviour and the social status of male and female subjects, as well as by genetic and hormonal differences.] We suggest that the juvenile marmosets tested

by Matoba et al. (1991) did not display handedness. There was a symmetrical distribution of left and right-hand preferences at the group level (Table 1, $\chi^2(2) = 0.61$, $p > 0.7$). Despite these objections to the statistical analysis of Matoba et al. (1991), they did present convincing evidence suggesting that hand preferences of marmosets (*Callithrix jacchus*) are strongly influenced by the preferences of their mothers: there was correlation with preferences of their mothers but not their fathers. Matoba et al. (1991) propose that the infants hand preferences may be genetically determined or may develop with experience, for example through imitation of the mother's hand use. In our colony of marmosets we have observed infants feeding from the hands of their parents and siblings throughout the first few months of life and we have also observed incidences of mothers protecting food sources to allow infants to feed but not the father or older siblings. These maternal influences may affect hand preferences, although that is not known.

We have scored hand use for holding food in a group of 21 marmosets and have found approximately equal numbers of left and right-hand preferent individuals. Of the 17 adult (older than 20 months), and 4 sub-adult marmosets that we tested, 13 were left-hand preferent and 8 were right-hand preferent (Table 1). We found no change in hand preference with age in a group of 11 marmosets tested from 3 to 22 months (Friedman statistic, $\chi^2 = 1.06$, $p = 0.79$; Hook-Costigan and Rogers, 1998). Similarly, Guerra and DaSilva (1996) report no evidence of handedness in feeding in a group of 9 *Callithrix jacchus* and 9 *Callithrix penicillata*. Therefore, there is no evidence of handedness for feeding in *Callithrix jacchus* or *Callithrix penicillata* despite previous suggestions that common marmosets (*Callithrix jacchus*) are left handed. It must be emphasised that although handedness is not present for the marmoset as a species, *Callithrix jacchus*, individuals do exhibit significant hand preferences (Table 1): approximately half of the marmosets are left handed and the other half are right handed.

In our study we have also recorded the posture assumed by the marmosets during each incidence of hand use in feeding. Generally, there were three postures adopted described as 1) tripedal, one hand and the two hindlimbs on the ground, 2) vertically seated, two hindlimbs and lower body on ground with forelimbs free and 3) suspended, the marmosets were suspended on wire mesh holding on with one hand and two feet. We calculated the percentage left-hand use in feeding displayed by 12 individuals for each category of posture. These individuals displayed at least 10 incidences of feeding in each posture. Intra-individual percentages of left-hand use were compared across

Table 1. Hand use for reaching for and holding food. Subjects were classified by age as: A, adults; S, subadults; J, juveniles; I, infants. Other abbreviations are: N, number of individuals; NA, individual data was not reported; NS, nonsignificant results (as reported in study or calculated using a chi square goodness-of-fit test); -, insufficient data to reach conclusion about direction of bias; L, left preference; R, right preference; Am, ambipreference. **These studies were conducted using the same colony of tamarins.

Species	Task	N	Age	Preference			Bias
				L	R	Am	
<i>Callithrix jacchus</i>							
Box (1977)	Taking food	4	A	3	1		-
		4	J	3		1	
	Holding food	4	A	2	1	1	-
		4	J	3	1		
Matoba et al. (1991)	Taking food	46	A	20	11	15	NS
		23	J	9	8	6	NS
Hook-Costigan & Rogers (1995 & unpublished data)	Holding food	17	A	11	6		NS
		4	S	2	2		
<i>Saguinus oedipus</i>							
Diamond & McGrew (1994)**	Holding food	20	10A, 7S, 3J		NA		Right p<0.001
	Food carry	20	10A, 7S, 3J		NA		Right p<0.001
King (1995)**	Taking food (objects)	30	A&J	7	21	2	Right p= 0.14
<i>Saimiri sciureus</i>							
Laska (1996a)	Taking food	12	8A, 4J	3	3	6	NS
<i>Ateles geoffroyi</i>							
Laska (1996b)	Taking food	13	10A, 3J	9	1	3	Left p<0.025
<i>Brachyteles arachnoides</i>							
Ades et al. (1996)	Holding, taking food	25-30	A, S & J		NA		Right 59% Left 22% Both 16%
<i>Cebus capucinus</i>							
Gomperts & Costello (1991)	Holding food	NA (Wild)	NA		NA		Right 67%
Masataka (1990)	Taking food	4	NA	1	3		-
<i>Cebus albifrons</i>							
Masataka (1990)	Taking food	3	NA		2	1	-

Table 1 Continued

Species Study	Task	N	Age	Preference			Bias
				L	R	Am	
<i>Cebus apella</i>							
Masataka (1990)	Taking food	24	NA	3	20	1	Right p< 0.01
Fragaszy & Mitchell (1990)	Holding, taking food	7	A	3	1	3	-
	Searching for food	7	A	3	2	2	-
Westergaard & Suomi (1993b)	Simple reach through holes	16	A	3	12	1	Right p<0.005
		5	J	5			-
Parr et al. (1997)	Taking food (quadrupedal)	13	A	3	3	7	NS
		9	J	1		8	
	Taking food (bipedal)	13	A	6	3	4	NS
		9	J	4		5	
Anderson et al. (1996)	Taking food	10	7A/S, 3J		NA		NS
Westergaard et al. (1997)	Taking food (quadrupedal)	28	20A, 8J	13	14	1	NS
	Taking food (bipedal)	28	20A, 8J	7	20	1	Right p<0.01

postures using the Friedman statistic (Siegel and Castellan, 1994) and no significant differences were found between the percentage left-hand use across the three postures ($\chi^2 = 1.61$, $p = 0.45$). Thus, posture has no significant influence on the direction of hand preferences in adult common marmosets, although we have some evidence to suggest that the strength and development of individual preferences may be affected by posture (Hook-Costigan and Rogers, in preparation).

Overall, it appears that the common marmoset does not have a population bias toward either right or left handedness although there might be a slight nonsignificant skew toward left-hand preferences. Age (3 to 22 months), gender and posture do not appear to affect the distribution of simple hand preferences in marmosets.

Tamarins (Saguinus oedipus)

In contrast to the marmoset, the closely related tamarin species (*Saguinus oedipus*) is right handed at the group level when holding food and picking up small objects including food and twigs (Table 1). Diamond and McGrew (1994) and King (1995) both used the same colony of tamarins (Diamond and McGrew (1994) tested 20 tamarins

and King (1995) tested 30 tamarins) and both found right handedness (Table 1). Diamond and McGrew (1994) reported that age, gender and family membership did not affect the distribution of hand preferences during feeding. King (1995) also reports that the distribution of the tamarins hand preferences was not related to age or gender, but he found a positive correlation between age and the degree of laterality displayed for taking food.

Posture does influence the direction of hand preferences in tamarins. Diamond and McGrew (1994) found a shift away from right-hand preferences when the tamarins (*Saguinus oedipus*) adopted an vertical posture during feeding. The authors suggested that this trend away from right handedness may reflect a trade off between using the more efficient forelimb for maintaining posture and the more efficient forelimb for performing the task. This result would appear to support the hypothesis of MacNeilage et al. (1987), as increased postural demands may have masked preferred hand use in the tamarins for picking up and holding food if they were right-hand preferent and used the right side of the body in postural control. King (1995) found no group bias, toward either right or left handedness, for vertical suspension by one hand and arm in the group of 30 tamarins (*Saguinus oedipus*; Table 1). He recorded the hand used to grip when a subject suspended its entire weight from one forelimb. There was increased incidence of left-hand preferences in the group (Table 1), but not a complete shift to left handedness, as MacNeilage et al. (1987) would have predicted.

Comparison between marmosets and tamarins

Different variables appear to influence the development and expression of hand preferences in the marmosets and tamarins. Although family membership was found to affect the development of directional hand preferences in the marmoset (Matoba et al. 1991), it did not influence the hand preferences of the tamarins (Diamond and McGrew, 1994). In addition, although the assumption of a vertical posture influenced the hand preferences of the tamarins, there was no effect of posture on the direction of hand preferences in the marmoset.

The hand preference distributions found for both marmosets and tamarins give little or no support to the Postural Origins hypothesis, even though lateralization for hand use during feeding differs for the two species. Neither species displays the left handedness postulated by MacNeilage et al. (1987). It could be argued that right handedness had already evolved in tamarins and that marmosets were in transition from

their left-handed ancestors (the prosimians) toward right handedness. However, the evolution of right handedness in tamarins fails to support the Postural Origins hypothesis as tamarins are fully arboreal and should, according to the hypothesis, require postural support by the stronger right side.

The fundamental difference between marmosets and tamarins is the evolution of modified lower anterior dentition for bark gouging in marmosets and not tamarins (Rosenberger, 1978; Ferrari, 1993). Although both tamarins and marmosets feed on plant exudates, the marmosets gouge holes while the tamarins use the holes made by other animals (Ferrari, 1993). The common marmoset (*Callithrix jacchus*) spends 15-29% of its foraging time gouging to extract gum exudate using the mouth as a foraging instrument rather than the hands (see Rylands and de Faria, 1993). To gouge tree trunks marmosets must cling to the trunk with both hands and both feet. This feeding adaptation may be one explanation for the lack of handedness in gouging marmosets and may explain the lack of effect of posture on hand preferences in marmosets, because both sides of the marmoset's body might require equal amounts of strength for clinging to the trunk. Lower amounts of use of the hands in acquiring food might lead to less evolutionary selection for handedness in the gouging species of marmosets. This hypothesis could be examined by comparing the distribution of hand preferences of *Callithrix jacchus*, a gouging marmoset species, with a distribution in another marmoset species, such as *Callithrix humeralifer*, that spends less of its foraging time tree gouging (see Rylands and de Faria, 1993). Other differences in foraging strategies of marmosets and tamarins may also contribute to their differences in handedness. Rylands and de Faria (1993) describe the marmosets foraging strategy as "a stealthy stalk and pounce, foliage-gleaning method", while Garber (1993) indicates that tamarins "...explore crevices and knotholes, rummage through palm fronds, jumping rapidly to ground to seize cryptic prey". These descriptions imply that the tamarins may employ a more manipulative strategy when foraging and when exploring crevices and knotholes, perhaps leading to increased right handedness in these species as suggested by MacNeilage et al. (1987). The leaping and landing employed in the tamarins foraging strategy may also affect their handedness perhaps leading to a division of function between the hands with one used to lead while leaping and the other, perhaps the right hand, to grasp the food object.

Squirrel monkeys (Saimiri sciureus), Spider monkeys (Ateles geoffroyi) and Muriquis (Brachyteles arachnoides)

Studies of hand use in feeding for other New World species including squirrel monkeys, spider monkeys and muriquis also fail to support the Postural Origins hypothesis. Only the spider monkey (*Ateles geoffroyi*) appears to show left handedness during feeding. Laska (1996b) found a significant bias for left handedness in a group of 13 spider monkeys when reaching from a tripedal posture for a raisin on the floor. However, on the same task Laska (1996a) found no evidence for handedness in a group of 12 squirrel monkeys (*Saimiri sciureus*). Instead, the hand preferences of the squirrel monkeys, as for the common marmoset, were symmetrically distributed at the group level. The hand preferences of the squirrel monkeys were not affected by age, gender, matriline or social rank (Laska, 1996a).

In contrast to both squirrel and spider monkeys, preliminary evidence indicates that wild muriquis, *Brachyteles arachnoides*, are right handed for taking and holding food (Ades et al. 1996; Table 1). The distribution of hand preferences of the muriquis did not appear to be influenced by age or gender but it was influenced by the posture assumed during feeding. Ades et al. (1996) recorded whether muriquis were feeding in sitting, standing or suspensory postures. In contrast to the tamarins, they found that right handedness was strongest when the muriquis fed in a standing posture, least when the subjects fed in a suspensory posture and intermediate when they fed in a sitting posture ($\chi^2(6) = 67.9, p < 0.01$). Ades et al. (1996) suggest that these results demonstrate intensification of pre-existing hand preferences when feeding in a more unstable standing posture.

Capuchins (Cebus spp.)

Westergaard et al. (1997) have reported that posture influences hand use in tufted capuchins (*Cebus apella*) also. The capuchins exhibited right handedness when they reached for food from a bipedal posture but not from a quadrupedal posture (Table 1) in which they kept both hindlimbs and one forelimb on the cage floor while reaching. There was an effect of age on the distribution of hand preferences during bipedal feeding: the right-hand preferences in adults were stronger compared to those of immatures. Increased right-hand use with increasing age has also been found in prosimians (Ward et al. 1993). There were no effects of either age or gender on directional hand preferences during feeding in a quadrupedal posture. Westergaard and

Suomi (1993a) also found right handedness in adult capuchins (*Cebus apella*) reaching for peanuts inside a container, but found left handedness in juvenile subjects (Table 1). The container the capuchins were required to reach into was 10 cm in diameter and only one type of food was presented, therefore we suggest that this task did not demand high levels of visuospatial processing (Westergaard and Suomi, 1993a). Other studies have also found that capuchins (*Cebus apella*, *Cebus albifrons*, *Cebus capucinus*) are right handed when collecting small pieces of food scattered on the floor (Masataka, 1990, see Table 1). The species *Cebus capucinus* may also be right handed as it uses the right hand twice as many times as the left when holding food (Gomperts and Costello, 1991; Table 1).

Parr et al. (1997) found no handedness in a group of 22 capuchins scored when they reached for food from both quadrupedal and bipedal postures (Table 1). More than 50% of subjects were ambipreferent in each of the postural conditions. They did, however, report that the number of lateralized subjects almost doubled when the capuchins were required to reach from a bipedal rather than quadrupedal posture (Table 1). Parr et al. (1997) concluded that the assumption of a bipedal posture may strengthen individual hand preferences in capuchins, although group level biases may not be influenced by bipedalism.

Two other studies of hand use in *Cebus apella* have not found right handedness. Anderson et al. (1996) report a mean percentage of left-hand use of 50% for a group of 10 capuchins scored when they adopted a quadrupedal posture to pick up food pellets from the floor. Unfortunately, this study did not report individual hand preferences. Fragaszy and Mitchell (1990) observed hand use in 7 capuchins when they were feeding in a seated position and searching for food in a quadrupedal posture. They found no evidence of a group bias for hand preference in either of these tasks (Table 1).

Overall, there appears to be a tendency toward increased right-hand preferences in feeding in *Cebus apella*, with 3 out of 6 studies reporting significant group biases. The 3 studies reporting right handedness in *Cebus apella* also had the largest number of subjects ($n > 20$; Table 1). Only Parr et al. (1997) did not find handedness with a sample size of more than 20 subjects. Nevertheless, the differences in handedness found across studies of capuchins, which all used similar methods to score hand preferences in feeding, suggests that other factors such as individual experience, familial relationships and housing conditions may influence lateralization in this species. Further research of hand preferences taking these variables into consideration is needed for all of the New World species.

Hand preferences during feeding in the platyrrhine species

There is evidence that tamarins, muriquis and capuchins display a tendency for right-hand preferences in feeding. Although the conclusion that these species have right handedness would be premature, the results do not support the hypothesis proposed by MacNeilage et al. (1987). There appears to be a shift toward right handedness, rather than left handedness, for feeding in the arboreal New World primates. In fact, the absence of handedness in the common marmoset and the squirrel monkeys also fails to support the hypothesis of MacNeilage et al. (1987). Only spider monkeys appear to be left-handed for feeding activities.

No evolutionary pattern emerges from the inconsistencies in hand preference between the platyrrhine species. Even the influences of age, gender and posture on hand preferences in platyrrhines appear to be species-specific. As handedness for food holding has been found in some studies, it cannot be said that hand use in feeding is simply too routine to elicit manual specialization as suggested by Fagot and Vauclair (1991). We suggested that hand use during feeding in New World primates may reflect the different motor, perceptual or cognitive demands of foraging strategies characteristic of a species. This hypothesis is discussed further in a later section of this review (see Conclusions and Comparisons with Prosimians, Old World Species and Apes).

VISUOSPATIAL REACHING PREFERENCES

Visuospatial reaching tasks require subjects to assess visually the spatial position of an object while reaching. Although hand use in feeding may require some degree of visuospatial processing, the tasks referred to as visuospatial are dependent on this form of processing. As neurophysiological evidence suggests that different neural pathways are involved in the perception of form and motion (Van Essen and Gallant, 1994), we divided the visuospatial tasks used with New World primates into two categories: 1) reaching for a static object (Table 2), and 2) reaching for a moving object (Table 3). Visual monitoring of moving objects also requires the analysis of the temporal aspects of the stimulus and may thus be more spatially complex than reaching for static objects.

Reaching for Static Objects

Hook-Costigan and Rogers (1995) scored the hand used by marmosets (*Callithrix jacchus*) when adopting a tripedal posture and reaching through holes in a clear perspex lid for assorted pieces of food in a bowl (Table 2 includes published as well as unpublished data by Hook-Costigan and Rogers). The subjects were required to assess spatial restrictions of hand holes while reaching and they also visually assessed the position of desired foods (ie. they looked for banana and cherries and avoided other pieces of fruit). [Note that this experiment differs from the previously mentioned one of Westergaard and Suomi (1993a), in which the subjects were required to reach for only one type of food and did not have to visually assess the spatial restrictions of hand holes. The latter study involved simple reaching.] In our study of 17 marmosets tested on the visuospatial bowl task there was no evidence of a group bias toward right or left-hand preferences (Table 2). Next the visuospatial and postural demands were increased by requiring the marmosets to reach for food on a plate held approximately 5 cm outside the cage while they maintained the vertical clinging posture, hanging on the wire mesh with one hand and two feet. Arm extension would increase the visuospatial demands by requiring visually guided movement using the proximo-distal musculature. Again, there was no evidence of handedness in this task (Table 2). Rothe (1973), however, found right handedness in marmosets (*Callithrix jacchus*) required to perform reaching tasks in tripedal and upright standing postures (Table 2). Unfortunately, Rothe (1973) did not report the results obtained in the different tasks and hand use in the two postures separately, but rather lumped the data into a category referred to as "handedness during the test series". Five of six tasks employed by Rothe (1973) required reaching for static objects and one test required the subjects to retrieve food from a swinging piece of string and from a moving platform. Overall, we can conclude that these six tests, cumulated by Rothe (1973), required visuospatial processing. The right handedness reported may have been due to the assumption of an upright posture (no details given) as our own study did not find handedness when marmosets reached for a static object in a tripedal posture (see above). Rothe (1973) seemed to have reported the results of his first test, requiring subjects to take a mealworm from a tube, independently of the other tests, but contradiction between his statement of methods, in which he indicates that he did not test juveniles, and the apparent results, in which juvenile preferences on the test are reported, does not allow us to elucidate exactly what was found.

Table 2. Visuospatial reaching for static objects. Abbreviations as in Table 1.

Species	Task Description	N	Age	Preference			Bias
				L	R	Am	
Study							
<i>Callithrix jacchus</i>							
Rothe (1973)	Pooled visuospatial reach (quadrupedal/ bipedal)	13 8	A J	5 1	8 6	1 1	Group-R: p<0.05
Hook-Costigan & Rogers (1995 & unpublished data)	Reach through holes	21	S	11	6	4	NS
	Vertical cling reach with extended arm	19	S	10	8	1	NS
<i>Saguinus oedipus</i>							
King (1995)	Extended reach	22	A&J	11	11		NS
	Ceiling suspended reach	22	A&J	8	14		NS
Roney & King (1993)	Vertical cling reach	14	A	6	8		NS
<i>Saimiri sciureus</i>							
King & Landau (1993)	Reach through pipe (quadrupedal / bipedal)	30	NA	12	11	7	NS
	Vertical cling reach	37	NA	7	24	6	R: p=0.004
Roney & King (1993)	Reach through holes (horizontal / vertical cling)	30	A, S&J	14	15	1	NS
Laska (1996a)	Vertical reach	12	8A, 4J	6	4	2	NS
<i>Ateles</i>							
Kounin (1938)	Extended reach	1	J		1		-
<i>Ateles geoffroyi</i>							
Laska (1996b)	Vertical reach	13	10A, 3J	10	1	2	Left: p<0.01
<i>Cebus</i>							
Kounin (1938)	Extended reach	3	S	1	2		-
<i>Cebus apella</i>							
Lacreuse & Fragaszy (1996)	Reach through holes	12	A	2	3	7	NS
		4	J	2	1	1	
		1	I			1	
Anderson et al. (1996)	Reach through holes	10	7A/ S, 3J		NA		NS
	Vertical cling reach	10	7A/ S, 3J		NA		NS
	Extended reach (vertical)	10	7A/ S, 3J		NA		NS
Fragaszy & Mitchell (1990)	Visually guided prehension	7	A	3	4		-
	Bimanual visually guided prehension (hand used to lift lid on box)	7	A	4	2	1	-

In a group of 6 marmosets, Hook-Costigan and Rogers (1995) found an inverse correlation between hand preferences displayed when taking food from the plate (described above) and side-of-mouth preferences when chewing a food bar ($r = -0.61$, $p = 0.05$). There was also significant positive correlation between hand preferences in feeding and the same side-of-mouth preferences displayed when chewing ($r = 0.70$, $p \leq 0.05$; Hook-Costigan and Rogers, 1995). On the basis of these results we suggested that marmosets may have a division of function between the hemispheres, at an individual level, with one hemisphere controlling hand use in feeding and side-of-mouth use in chewing and the other visuospatial reaching. This division of function was not found in a second group of 11 marmosets. However, the marmosets in the second group had more stable preferences (with changing age) than that of the first group (Hook-Costigan and Rogers, in preparation). The first group received less parental care and were housed in more stressful conditions before coming to our laboratory. Thus, we have deduced that variables such as the degree of parental care experienced as juveniles, arousal and housing conditions may affect the development and expression of hand preferences in marmosets. Hand preferences may be learnt from parents as suggested by Matoba et al. (1991). These variables should be considered in all studies of lateralization.

Absences of handedness have also been reported for tamarins tested in tasks requiring them to adopt a suspensory posture to reach for static objects. King (1995) scored hand preferences in the tamarins (*Saguinus oedipus*) suspending their entire weight from the ceiling (upside down) to reach for food. He found no evidence of a group bias in this task (Table 2). Nor did he find handedness when the tamarins were required to reach for a piece of food set on a disc outside their cage (Table 2), although all of the subjects tested displayed significant hand preferences on both tasks (Table 2). Next King (1995) introduced novel postural demands by requiring the subjects to reach for a static object when standing on stable and unstable platforms, which were alternated between testing sessions. Neither postural condition resulted in handedness in the group (King, 1995). Similarly, Roney and King (1993) did not find a bias for right or left handedness, or an effect of posture, on visuospatial reaching preferences in 14 tamarins (*Saguinus oedipus*) required to reach with an extended arm for food. They found that 6 tamarins were left-hand preferent and 8 were right-hand preferent when reaching for food from both quadrupedal and vertically suspended postures (Table 2).

King and Landau (1993) did not find handedness in squirrel

monkeys (*Saimiri sciureus*) reaching for a static food object when they were adopting a bipedal or quadrupedal posture (Table 2), but they did find right handedness when the squirrel monkeys were required to maintain a vertically suspended posture while reaching (Table 2). These results were not replicated in subsequent tests requiring vertical clinging even though 24 of the same subjects were tested (Roney and King, 1993). A bimodal distribution of hand preferences was found (Table 2). Roney and King (1993) argued that the different distributions of hand preferences in the two experiments may have been due to alternation between reaches from a quadrupedal and vertical posture, a condition introduced in the second experiment. Laska (1996a) reported an increased incidence of individual hand preferences when squirrel monkeys were required to reach from an unsupported bipedal posture for food placed above them, compared to hand preferences when feeding in a quadrupedal posture, although there was no handedness within the group for either task (Tables 1 and 2). Overall, these results suggest that squirrel monkeys may display right handedness when reaching for static objects from a vertical clinging posture and are ambipreferent when they reach from quadrupedal or bipedal postures.

As for hand preferences in feeding activities, spider monkeys (*Ateles geoffroyi*) display left handedness when reaching from an erect bipedal posture for a raisin placed outside the cage (Table 2). The subjects were able to support themselves with one hand on this task. Ten of the 11 spider monkeys that displayed significant preferences on this task were left handed. Laska (1996b) found that the hand use of the spider monkeys on this task did not differ significantly from that displayed during feeding activities.

Studies of capuchins requiring simple reaching through holes to retrieve food have not found handedness (Lacreuse and Frigaszy, 1996; Anderson et al. 1996). Anderson et al. (1996) reported an increase in strength of individual preferences when subjects assumed a vertical clinging posture while reaching, rather than a sitting position. Employing more difficult visually guided prehension tests, Frigaszy and Mitchell (1990) also found that no handedness occurred in capuchins, although they acknowledged that their sample size of 7 subjects was too small to draw conclusions (Table 2).

Overall, these data indicate that either a bimodal distribution of hand preferences or right handedness occurs during static reaching tasks in the New World species. Arm extension does not appear to influence handedness, but the posture assumed while reaching does influence the strength and possibly direction of individual preferences in marmosets,

squirrel monkeys and capuchins. As for hand use in feeding, the effect of posture on hand preferences scored when reaching for static objects is species-specific.

Reaching for a Moving Object

Hook-Costigan and Rogers (1995) conducted two tasks requiring common marmosets to reach for a moving object (Table 3). Postural demands and arm extension were required in a task that involved reaching to catch a swinging piece of string (approximately 5 cm outside the cages) while maintaining a vertical clinging posture. As for the static reaching tasks, there was no evidence of handedness in this task (Table 3). Similarly, neither marmosets (*Callithrix jacchus*) nor tamarins (*Saguinus oedipus*) demonstrate handedness when required to retrieve food from rotating discs (Hook-Costigan and Rogers, 1995 and unpublished data; King, 1995). Both species display bimodal distributions of hand preferences (Table 3).

Only one test of visuospatial reaching for moving objects has demonstrated left handedness, as proposed by MacNeillage et al. (1987). King and Landau (1993) reported left handedness in a group of 10 squirrel monkeys (*Saimiri sciureus*) required to catch live fish from wading pools (Table 3).

There have been too few studies of hand use when reaching for moving objects in the New World primates to determine whether these species have manual specialization for these tasks. To date, to the authors' knowledge, there have been no studies investigating hand preferences of capuchins when reaching for moving objects. While Westergaard and Suomi (1996) have scored the hand preferences of 4 capuchins throwing stones (Table 6) there has been no examination of catching behaviour in this species.

HAND PREFERENCES FOR HAPTIC EXPLORATION AND TACTUALLY GUIDED REACHING

Only four studies have examined hand preferences for haptic discrimination and tactually guided reaching in the New World primates. These studies tested capuchins (*Cebus apella*), spider monkeys (*Ateles geoffroyi*) and squirrel monkeys (*Saimiri sciureus*). Lacreuse and Frigaszy (1996) scored 21 capuchins in a task requiring the subjects to explore without visual guidance clay objects of different shapes (eg. star, sphere) in order to find sunflower seeds embedded in them. They found significant left handedness in the group (Table 4) and

Table 3. Visuospatial reaching for moving objects. Abbreviations as in Table 1.

Species	Task Description	N	Age	Preference			Bias
				L	R	Am	
Study							
Callithrix jacchus							
Hook-Costigan & Rogers (1995 & unpublished data)	Extended reach to grasp swinging string	17	S	10	6	1	NS
	Rotating disc task	17	A	8	7	2	NS
Saguinus oedipus							
King (1995)	Rotating disc task	21	A&J	8	8	5	NS
Saimiri sciureus							
King & Landau (1993)	Fishing from bowls	16	NA	11	3	2	NS
	Fishing from wading pools	10	NA	8		2	Left p= 0.013

Table 4. Hand use in haptic exploration and tactually guided tasks. Abbreviations as in table 1.

Species Study	Task Description	N	Age	Preference			Bias
				L	R	Am	
<i>Saimiri sciureus</i>							
Laska (1996a)	Vertical reach	12	8A, 4J	6	6		NS
Laska (1996a)	Tactual vertical reach	12	8A, 4J	5	6	1	NS
<i>Ateles geoffroyi</i>							
Laska (1996b)	Tactual reach	13	10A, 3J	10	1	2	Left p<0.025
<i>Cebus apella</i>							
Parr et al. (1997)	Haptic exploration (objects in pine-shavings)	13	A	11	2		Left
		9	J	4	1	4	p<0.01
	Haptic exploration (objects in water)	22	13A, 9J	15	2	5	Left p<0.01
Lacreuse & Fragaszy (1996)	Haptic exploration	12	A	7	2	3	Group-
		6	J	2	2	2	Left
		3	1	3			p<0.05

there was no effect of object shape on the hand preferences. Lacreux and Fragaszy (1996) found an effect of gender on hand preferences in this task; females showed significant handedness at a group level but males did not. They suggest that this effect was primarily due to the adult male subgroup ($n = 3$) in which two subjects were right-hand preferent and one was ambipreferent. No similar shift in handedness was found in the female subjects.

Parr et al. (1997) also found left handedness for performance of a haptic discrimination task by capuchins. However, they found no effect of age or gender on the hand preferences of the subjects. Fourteen of 22 individuals preferred to use the left hand to locate food hidden in pine-shavings (Table 4). Moreover, 15 of the subjects displayed left-hand preferences when required to locate food in water and there was a significant shift toward stronger left-hand preferences. The increased left-hand use may have been caused by increased difficulty during prehension of an object in a water substrate or as the authors suggest may have been due to decreased visual cues in the second condition. The subjects were able to view the contents of the box of pine-shavings through the hand hole before they reached in the first condition, by contrast they could not see objects in the water through the arm hole.

Laska (1996b) has also found evidence of left handedness in spider monkeys during tactually guided reaching (Table 4). The subjects were required to locate a raisin at the bottom of an opaque tube without visual guidance. The subjects had to assume a squatting bipedal posture to reach into the tube. Eleven of the 13 subjects tested displayed significant left-hand preferences on this task and 2 were right-handed. It is interesting to note that Laska (1996b) found no significant differences between hand preferences displayed in feeding activities, visually guided reaching or tactually guided reaching.

However, Laska (1996a) found no evidence of handedness for tactually guided reaching in a group of 12 squirrel monkeys on a similar task to that used with the spider monkeys (Table 4). The squirrel monkeys were required to reach into a tube to grasp a raisin while maintaining an erect bipedal posture. The hand preferences displayed by the squirrel monkeys were, however, stronger in the tactually guided reaching tasks than in the visually guided tasks performed with the same subjects (Table 2). There were no effects of age, gender or family membership on hand preferences in the tactually guided reaching task. It would appear that the postural demands in this task affected the hand preferences of the squirrel monkeys.

Therefore capuchins, and perhaps spider monkeys, appear to have

specialization of the right hemisphere (left hand) for the fine digital exploration of objects while squirrel monkeys have no specialization for this type of hand use. Alternatively, manual specialization for haptic exploration may not emerge when subjects are required to grasp a single object, such as a raisin, perhaps using a power grip, as in the task used for the squirrel monkeys. Tactual exploration may be necessary to elicit handedness for this type of manual function. Whether the left handedness displayed by the group of spider monkeys tested on a task similar to that used for the squirrel monkeys is indicative of a right hemisphere specialization for haptic exploration remains to be discerned. To evaluate hemispheric differences the movement of the digits needs to be noted in haptic discrimination tasks. Also, haptic exploration tasks must be employed with the other New World species, including marmosets and tamarins, before it will be possible to hypothesize how this type of manual specialization may have evolved.

MANIPULATIVE HAND USE AND TOOL USE PREFERENCES

Tool using was once believed to be a characteristic unique to humans, but there is increasing evidence of tool using by other species, including nonhuman primates, elephants and birds (Goodall, 1964; Beck, 1980; Rogers and Kaplan, 1993; Chevalier-Skolnikoff and Liska, 1993; Petit and Thierry, 1993; Nishida and Nakamura, 1993; Tokida et al. 1994; Hunt, 1996). However, the capuchins are the only New World species so far reported to use tools. Westergaard and Suomi (see Table 5) have observed the use of hammering, sponging and probing tools by captive capuchins (*Cebus apella*). They reported a bias toward right-hand preferences for adults during sponging activity (Westergaard and Suomi, 1993a). They also suggested that right handedness may increase with age, as 7 of the 9 adult subjects tested displayed right-hand preferences when using sponges, while 3 of 5 juveniles displayed left-hand preferences and 2 were ambipreferent (Table 5). The adults displayed a stronger mean lateral bias than the juvenile subjects.

Westergaard and Suomi (1993b) found that juvenile capuchins (*Cebus apella*) used bimanual striking actions more than adults when they were required to use nut cracking tools, although they found no significant differences in the strength or direction of hand preferences between the age groups (Table 5). On this task they found a tendency toward left-hand preferences in the group as a whole and proposed that

Table 5. Hand preferred during using of tools. Abbreviations as in Table 1.

Species Study	Task Description	N	Age	Preference			Bias
				L	R	Am	
<i>Cebus apella</i>							
Westergaard et al. (1993a)	Sponging task	9	A	2	7		Adults toward Right
		5	J	3		2	
Westergaard et al. (1993b)	Nut cracking	7	A	3	3	1	Toward left
		7	J	5	1	1	
Westergaard (1991)	Probing: Insert probe	4	A	3	1		-
		1	J	1			
	Probing: Remove probe	4	A	2	1	1	-
		1	J	1			
	Probing: Feed from probe	4	A	3	1		-
		1	J	1			
Anderson et al. (1996)	Probing: Insert probe (sitting, standing)	1	7A/S, 3J		NA		NS
		0					
	Probing: Insert probe (vertical cling)	1	7A/S, 3J		NA		NS
		0					

this bias may be due to increased spatial processing which would be necessary to accurately hit a nut. They also reported that, when striking nuts, female capuchins displayed stronger right-hand biases than males. This contrasts with the absence of gender differences in other studies of capuchins during feeding activities and for use of sponging and probing tools (Westergaard, 1991; Masataka, 1990; Westergaard and Suomi, 1993a).

Westergaard and Suomi (1994) also reported an increased incidence of unilateral hand use of probing tools by adult capuchins (*Cebus apella*) compared to juveniles. They found that unimanual manipulation emerged in capuchins between 3 and 5 years of age. Regrettably, however, these authors did not report the direction of hand preferences in this particular study.

Westergaard (1991) reported that 4 out of 5 capuchins were left-hand preferent and one was right-hand preferent for inserting and feeding from a probe (Table 5). He suggested that the tendency toward left-hand preferences in this study may be indicative of specialization of the right hemisphere for spatial processing, a proposal needing to be confirmed in a larger sample. A later study by Anderson et al. (1996) reported stronger left-hand use, compared to hand preferences measured during feeding and in visuospatial tasks (Tables 1 and 2), in a group of 10 *Cebus apella* observed when inserting a baton through a

Table 6. Other measures of hand preferences. Abbreviations as in Table 1.

<i>Species</i>	Task Description	N	Age	Preference			Bias
Study				L	R	Am	
<i>Callithrix jacchus</i>							
Stellar (1960)	Displace an object	8	NA	2	4	2	-
<i>Saimiri sciureus</i>							
Costello & Fragaszy (1988)	Unimanual grasp (object in view/ out of view, embedded)	6	A	4	2		-
<i>Ateles</i>							
Kounin (1938)	Open box, hold lid and take food with one hand	1	J		1		-
	Retrieve food with a rake	1	J	1			-
<i>Cebus</i>							
Kounin (1938)	Open box, hold lid and take food with one hand	3	S	1	2		-
	Retrieve food with a rake	3	S	1	2		-
<i>Cebus apella</i>							
Costello & Fragaszy (1988)	Unimanual grasp (object in view/ out of view, embedded)	6	A	2	4		-
Westergaard & Suomi (1996)	Stone throwing	4	3A, 1J	2	1	1	-

hole and into a tube to obtain honey, although they found no significant bias for handedness at the group level. These authors did not report individual hand preferences. Anderson et al. (1996) also reported postural affects on handedness in the probing task, demonstrating that increased left-hand use was evident only when the capuchins were required to maintain a vertical clinging posture.

Costello and Fragaszy (1988) report that, in a group of 6 capuchins (*Cebus apella*), 4 subjects displayed right-hand preferences when reaching for and grasping objects and 2 displayed left-hand preferences (Table 5). When using a precision grip 3 of the 4 subjects that had displayed overall right-hand preferences for reaching and grasping again displayed right-hand preferences and the fourth subject displayed more right than left-hand use, but the preference was not significant. The two subjects that displayed left-hand preferences for reaching and grasping did not show a significant hand preference when using a precision grip. Costello and Fragaszy (1988) also reported that the

subjects that preferred the right hand in reaching were more likely to take an object using a precision grip, rather than a power grip, while left-handed subjects did not favour either a precision or power grip when prehending an object. The authors' suggest that these results may be indicative of increased right-hand use in capuchins when fine sensorimotor control is required, but, of course, larger sample sizes are needed.

At present, results for the different types of tool using tasks employed with capuchins suggest left hemisphere specialization for manipulative tool using tasks. This may, possibly, be the case in sponging, which may require precise finger positioning and grip strength in order to absorb a fluid and to squeeze it into the mouth, although this has not been scored. There is also some evidence for increased right-hand use when capuchins grasp objects with precision grips (Costello and Frigaszy, 1988). The right hemisphere may be specialized for tasks demanding high levels of spatial processing, such as nut cracking and probing (Westergaard, 1991; Westergaard and Suomi, 1993a,b). Further research with larger samples are needed to confirm the biases reported. However, there is indication that tool using and right handedness may have evolved before bipedalism, and well before the apes and, indeed, humans evolved.

HAND USE IN ROUTINE ACTIVITIES OTHER THAN FEEDING

Hand use in routine activities, such as grooming, object exploration and play, have been referred to as "spontaneous hand use" by a number of researchers (eg. Diamond and McGrew, 1994; Rothe, 1973). However, these activities should be distinguished from hand use in feeding, as they might require different levels of manipulative control.

Rothe (1973) found no evidence for handedness in marmosets, most of the subjects being ambipreferent, but he lumped into a single category hand using behaviours as diverse as food holding, grooming, play and object exploration (Table 7). We suggest that the predominance of ambipreference in Rothe's (1973) study may have been the result of cumulating the data across this variety of hand use behaviours. In fact, Box (1977) reported that more than 50% of individuals were ambipreferent when she scored hand use in climbing, walking and hitting other subjects (Table 7). Differences in hand preferences displayed across simple acts of hand using have also been reported for orangutans: orangutans (*Pongo pygmaeus pygmaeus*) display left handedness when touching the face but no handedness for

food holding (Rogers and Kaplan, 1996).

The consistency of hand preference across routine manual activities may be another way in which marmosets and tamarins differ. Diamond and McGrew (1994) found that tamarins are significantly right handed for retrieving food, holding food, carrying food, self grooming, grooming others and hitting other individuals (Tables 1 and 7). In fact, the tamarins displayed ambipreference only when scratching themselves. Age, gender and family membership did not affect the hand preferences of the tamarins in any of the activities. However, as for the feeding activities, there was a shift away from right-hand preferences in the tamarins when they performed routine tasks, other than feeding, while adopting an upright posture. In the upright posture right handedness was only maintained for hitting other individuals.

Arguette et al. (1992) found that only 2 individuals, in a group of 13 squirrel monkeys (*Saimiri sciureus*), had significant right-hand preferences for self-directed touches (Table 7), but all of the subjects did, in fact, perform more touches with the right hand than the left, indicating a tendency for right-hand use in the group as a whole. This method of analysis is, however, not entirely satisfactory. Despite this, it is interesting to note that the preferred hand for self-touching may be opposite in orangutans and squirrel monkeys.

Overall, the lack of data on the different forms of routine manual activities makes it impossible to postulate whether handedness is present for these behaviours in the New World species.

CONCLUSIONS AND COMPARISONS WITH PROSIMIANS, OLD WORLD SPECIES AND APES

The reported hand preferences in the New World species do not support the hypothesis proposed by MacNeilage et al. (1987). Instead, some of the platyrrhine species demonstrate right handedness during feeding activities and others including the common marmoset (*Callithrix jacchus*) and squirrel monkeys (*Saimiri sciureus*) do not display handedness in feeding. Only one New World species, the spider monkey (*Ateles geoffroyi*), displays left handedness as would be predicted by the Postural Origins hypothesis. We suggest that a different feeding strategy, gouging of gum exudates, used by the common marmoset (Ferrari, 1993) places more emphasis on mouth use to acquire food and may have been a factor influencing the absence of handedness in the common marmoset and other marmosets that gouge, in comparison to the other New World primates. The hand preferences of other species of marmoset such as *Cebuella pygmaea*, *Callithrix*

Table 7. Hand preferred in routine activities other than feeding.
Abbreviations as in Table 1.

Species Study	Task Description	N	Age	Preference			Bias
				L	R	Am	
<i>Callithrix jacchus</i>							
Rothe (1973)	Simple hand use (pooled)	13	A	1	4	8	NS
		8	J	1	2	5	
Box (1977)	Reaching up	4	A		1	3	-
		4	J	1	1	2	
	Reaching down	4	A			4	-
		4	J			4	
	Walking	4	A		1	3	-
		4	J	1		3	
	Climbing up	4	A		1	3	-
		4	J			4	
	Hit	4	A	1		3	-
		4	J		2	2	
<i>Saguinus oedipus</i>							
Diamond & McGrew (1994)**	Self groom	20	10A, 7S, 3J		NA		Right p<0.001
	Social groom	20	10A, 7S, 3J		NA		Right p<0.001
	Scratch	20	10A, 7S, 3J		NA		NS
	Hit	20	10A 7S, 3J		NA		Right p<0.001
King (1995)	One arm suspension	30	A&J	17	10	3	NS
<i>Saimiri sciureus</i>							
Arguette et al. (1992)	Self touching (body)	13	A		2	11	NS
<i>Cebus apella</i>							
Fragaszy & Mitchell (1990)	Social grooming	3	A	2		1	-

humeralifer and *Callithrix penicillata* needs to be assessed. Similarly, it has been proposed that hand preferences in other New World species may be influenced by the perceptual, cognitive and motor demands of their particular foraging strategies.

In addition, while there is some evidence of left handedness for tasks demanding high levels of spatial processing when reaching for a moving object (King and Landau, 1993), hand use appears to be task specific. The limited number of studies reporting this type of hand use makes it difficult to discern the factors affecting the expression of this type of manual asymmetry. In studies reporting visuospatial reaching

for static objects, the New World primates appear to display right handedness, a symmetrical distribution of preferences at a group level or left handedness, for the spider monkeys, which resembles the results for hand use in feeding more than those for reaching for moving objects.

There is evidence that capuchins, and perhaps spider monkeys, display left handedness for haptic discrimination (Lacreuse and Frigaszy, 1996; Parr et al. 1997; Laska, 1996b). Left handedness for haptic discrimination has also been reported for rhesus monkeys (Fagot et al. 1991) and for humans (Hermelin and O'Connor, 1971; Flannery and Balling, 1979). Capuchins also display right handedness in tasks requiring fine motor control and manipulation (Costello and Frigaszy, 1988; Westergaard et al. 1993a) and an increased incidence of left-hand use on tasks with increased spatial demands such as probing (Westergaard, 1991; Anderson et al. 1996). Overall, like humans, capuchins appear to be right handed for most tasks but left handed for haptic discrimination and complex spatial tasks.

Several variables may affect the distribution and strength of hand preferences in the New World primates. These are age, gender and posture, but the effects of age on the development of manual preferences in primates are still unclear. In studies of prosimians, Old World primates and great apes, some researchers have found increases in strength of manual preference with increasing age (Lehman, 1978; Brooker et al. 1981; Forsythe and Ward, 1988; Mason et al. 1995; Toonoka and Matsuzawa, 1995), others suggest shifts in hand preferences with age (Sugiyama et al. 1993; Fagot et al. 1991; Hopkins et al. 1993; Rogers and Kaplan, 1996) and yet others report no affect of age on hand preferences (Vauclair and Fagot, 1987; Fagot and Vauclair, 1988; Fagot et al. 1991; Hopkins, 1993; Colell et al. 1995). Similarly, the influence of age on hand preferences in the New World primates varies. Some of the studies of hand use in the platyrrhine species report no affect of age on lateralization (Diamond and McGrew, 1994; Ades et al. 1996), whereas others have found that age affects lateral hand preferences in these species (Westergaard and Suomi, 1993a; King, 1995; Lacreuse and Frigaszy, 1996; Westergaard et al. 1997). An increase in right handedness with age has been found for capuchins in a variety of tasks including hand use when feeding in a bipedal posture (Westergaard et al. 1997), hand use when reaching for a static object (Westergaard and Suomi, 1993a) and hand use while using sponges to absorb juice (Westergaard and Suomi, 1993a). Lacreuse and Frigaszy (1996) also reported increased right handedness in adult male capuchins

in a test of haptic exploration, conversely they found no shift to right handedness with age in females but, in fact, adult females displayed stronger left-hand preferences than juvenile females. By contrast, Parr et al. (1997) found that neither age or gender influenced hand preferences of capuchins on their haptic discrimination task. Overall, while age may increase handedness in capuchins, there do not appear to be consistent effects of age on lateralization across tasks or groups of subjects in the other New World primates. Consideration of other variables in addition to age, such as individual history or experience, familial relationships, housing conditions (Deuel and Dunlop, 1980) and the disposition of the subjects at the time of testing may allow for more conclusive analyses of developmental effects on lateralization. Clearly, age is a variable that needs to be stated in all studies of handedness.

The gender composition of a population has also been suggested as a variable that may affect handedness distributions (Ward et al. 1993). Overall, however, very few studies have reported an effect of gender on hand preferences in nonhuman primates. Most of the reports of gender effects on handedness are for prosimians, increased left-hand preferences occurring in males compared to females (Milliken et al. 1989; Milliken et al. 1991; Mason et al. 1995). A study of hand use during feeding in Old World species *Rhinopithecus* and *Presbytis* suggested that males display right handedness while there is a symmetrical distribution of hand preferences in females (Yuan et al. 1986). Yet, the majority of studies of Old World primates and the great apes have reported no relationship between gender and hand preference distributions (Brooker et al. 1981; Vauclair and Fagot, 1987; Annett and Annett, 1991; Fagot et al. 1991; Hopkins, 1993; Hopkins et al. 1993; Colell et al. 1995; Tonooka and Matsuzawa, 1995). As for Old World primates, most studies of the New World primates have reported no influence of gender on the distribution of hand preferences (Masataka, 1990; Westergaard, 1991; Westergaard and Suomi, 1993a; Diamond and McGrew, 1994; King, 1995; Ades et al. 1996; Westergaard et al. 1997). Only two studies with capuchins have reported gender effects on hand preferences (Lacreuse and Frigaszy, 1996; Westergaard and Suomi, 1993b). Westergaard and Suomi (1993b) report stronger lateralization in female than male capuchins during a nut cracking task, while Lacreuse and Frigaszy (1996) found differential effects of age according to the gender of the subjects on haptic discrimination preferences as discussed above. We would suggest that effects of gender on hand preference may be secondary to

other variables such as social status and age.

As MacNeilage et al. (1987) have stated, the posture adopted during hand use appears to be the most influential variable on handedness in the New World primates. There is evidence that increasing postural instability increases handedness across tasks and across species, but postural effects appear to be species-specific. The direction of hand preferences in marmosets do not appear to be influenced by posture (Hook-Costigan and Rogers, unpublished data) although there is some evidence to suggest that right-hand preferences may emerge in this species, perhaps with the assumption of a bipedal posture (Rothe, 1973). By contrast, right handedness decreased in tamarins when they performed daily hand using activities in a bipedal stance (Diamond and McGrew, 1994) and when they reached from suspended postures (Roney and King, 1993; King, 1995). Squirrel monkeys display stronger hand preferences when reaching from a suspended posture than they do from quadrupedal or bipedal postures (King and Landau, 1993; Roney and King, 1993). Ades et al. (1996) report that wild muriquis displayed a stronger right-hand bias for feeding when standing compared to sitting or suspended. Capuchins also display stronger handedness when stability is decreased during feeding, reaching and in tool using (Anderson et al. 1996; Westergaard et al. 1997). This strong affect of posture is not limited to the New World species; there is also evidence of postural effects on lateral hand use in other primates, including prosimians, Old World species and apes (Sanford et al. 1984; Larson et al. 1989; Forsythe and Ward, 1988; Milliken et al. 1991; Fagot et al. 1991; Hopkins et al. 1992; Dodson et al. 1992; Ward et al. 1993; Hopkins, 1993; Devleeschouwer et al. 1995). Unstable postures appear to intensify hand preferences, perhaps by increasing arousal (Ward et al. 1993) or the spatiotemporal requirements of a task (Fagot and Vauclair, 1991).

Overall, posture appears to be a very important influence on the expression of hand preferences, as MacNeilage et al. (1987) suggested. In fact, in accordance with the hypothesis of MacNeilage et al. (1987), the assumption of a vertical posture appeared to increase right-hand use in squirrel monkeys (King and Landau, 1993), muriquis (Ades et al. 1996) and capuchins (Westergaard et al. 1997). However, these reports are contradicted by evidence suggesting an opposite effect of vertical posture in tamarins (Diamond and McGrew, 1994). We suggest that, if bipedalism does increase handedness in a species, it intensifies pre-existing specializations (Roney and King, 1993). This would indicate that specialization of the left hemisphere for manual tasks, that do not

demand high levels of visuospatial or haptic processing, may be present in some arboreal New World primates, contradicting the hypothesis of MacNeilage et al. (1987).

The predominance of right handedness among the New World primates is contrasted by reports of left handedness in prosimian populations (Sanford et al. 1984; Forsythe and Ward, 1988; Masataka, 1989; Ward et al. 1990; Milliken et al. 1991). Adaptation to the New World environment and the evolution of manipulative feeding strategies may have led to an evolutionary shift in hemispheric dominance.

The relative importance of the majority of individuals in a species being lateralized in the same direction needs to be addressed. MacNeilage et al. (1987) suggested that handedness evolved to overcome problems of postural control when feeding because there was a need for a division of function between the hands, but it is not clear why all members of a species need to be lateralized in the same direction. We suggest that handedness may have evolved as a consequence of pre-existing specializations that were present for communication, both vocal and visual.

It has been suggested that the hand preferences, or handedness, of the different New World primate species may reflect underlying hemispheric specializations for perceptual or cognitive processes or, indeed, other motor behaviours. Recent findings of cognitive (Horster and Ettlinger, 1985; Hopkins et al. 1992; Hopkins and Washburn, 1994), social (Stafford et al. 1990) and temperamental differences (Hopkins and Bennett, 1994; Watson and Ward, 1996) between left and right-handed primates also indicate that directional hand use may reflect other aspects of temperament or cognitive function on which selective pressures may operate. Handedness may also reflect a form of social communication conveying information about the nature of the sender. Alternatively, Walker (1987) suggested that right handedness may have evolved through generalization of specializations involved in the initiation of muscular movements, subjected to a pre-existing left hemisphere specialization for production of vocal signals. There is increasing evidence of hemispheric specializations analogous to humans for perception and production of species-specific vocalizations involved in social contact and affective communication in species throughout the evolutionary continuum from fish to chimpanzees (Petersen et al. 1978; Nottebohm et al. 1979; Petersen et al. 1984; Heffner and Heffner, 1984; Ehret, 1987; Fitch et al. 1993; Fine et al. 1996; Bauer, 1993; Berntson et al. 1993; Hollman and Hutchison, 1994; Hauser and Andersson, 1994; Hook-Costigan and Rogers, unpublished

material reviewed in Rogers and Bradshaw, 1996).

Further research investigating other types of lateral asymmetries in nonhuman primates is essential to understanding how and why lateralization evolved. We would suggest that handedness did not simply evolve spontaneously to overcome problems of postural control when feeding. Although posture does appear to affect hand use in many species, it seems to intensify lateral preferences rather than change the direction of lateralization. In addition, there is no evidence for consistent postural differences between prosimians and many of the arboreal New World species, although their hand preferences are clearly different. Relationships between handedness and lateralities related to communicative function and perceptual functions, including eyedness and processing and production of species-specific vocalizations in New World species, need to be examined (Hook-Costigan and Rogers, 1997; Hook-Costigan and Rogers, submitted). In addition, lateral hand use has not been examined in many New World species including *Aotes*, *Pithecia*, *Chiropotes*, *Cacajoa*, *Alouatta* and *Lagothrix*. Data on the distribution of hand preferences in these species may provide further clues about the evolution of hand use asymmetries in the New World primates.

To date, the New World species have been somewhat neglected in lateralization studies, perhaps because they are not considered to be in the direct ancestral lineage of humans. However, we suggest that these species may provide valuable information with regard to the evolution and nature of hemispheric specialization.

ACKNOWLEDGEMENTS

This research forms part of M.A Hook-Costigan's PhD degree and she acknowledges the support of a University of New England Research Scholarship. L.J. Rogers gratefully acknowledges support from the Australian Research Council (Grant No. A 09330984).

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